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Utilization of alien genes to enhance Fusarium head blight resistance in wheat – A review

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Summary

Fusarium head blight (FHB) is a destructive disease of wheat worldwide. Sources of resistance to FHB are limited in wheat. Search for novel sources of effective resistance to this disease has been an urgent need in wheat breeding. Fusarium head blight resistance has been identified in relatives of wheat. Alien chromatin carrying FHB resistance genes has been incorporated into wheat through chromosome addition, substitution, and translocation. Relatives of wheat demonstrate a great potential to enhance resistance of wheat to FHB.

Introduction

Fusarium head blight (FHB), also known as scab, is an important disease of all classes of wheats (*Triticum* L.) worldwide. It is caused mainly by the fungus *Fusarium graminearum* Schwabe (teleomorph *Gibberella zeae* (Schw.) Petch). Epidemics of this disease can result in significant economic losses for wheat growers in terms of yield and quality (McMullen et al., 1997; Nganje et al., 2001). Another serious concern with FHB is the contamination of wheat grain with mycotoxins produced by the pathogen. Mycotoxin-contaminated wheat may not be suitable for human consumption (Bai et al., 2001; Windels, 2000). Therefore, FHB can be a serious threat to the producers, processors, and consumers of wheat. Extensive efforts have been made worldwide to minimize the losses caused by this devastating disease in wheat (Rudd et al., 2001).

Effective cultural practice and chemicals are not available to control FHB in wheat. Host resistance has been considered a practical and effective means to combat FHB in wheat. However, only limited sources of partial resistance to FHB have been identified in common wheat (*T. aestivum* L., $2n = 6x = 42$, AABBDD), such as the Chinese cultivar ‘Sumai 3’ and its derivatives, the Brazilian cultivar ‘Frontana’, and the Eastern European germplasm ‘Praag 8’ (Mentewab et al., 2000). Effective resistance to FHB has not been found in durum wheat (*T. turgidum* L. var. *durum*, $2n = 4x = 28$, AABB). Only partial resistance has been identified from wild tetraploid wheat species, *T. dicoccoides* (Körn. ex Asch. & Graebner) Thell. ($2n = 4x = 28$, AABB) (Miller et al., 1998; Stack et al., 2002; Buerstmayr et al., 2003).

Resistance to FHB has been classified into five types: (1) resistance to initial infection, (2) resistance to spread of infection within a spike, (3) decomposition or non-accumulation of mycotoxins, (4) resistance to kernel infection, and (5) yield tolerance (Schroeder & Christensen, 1963; Wang & Miller, 1988; Mesterhazy, 1995). Lack of effective resistance sources hinders development of cultivars highly resistant to FHB in both common wheat and durum. Complex inheritance of FHB resistance in various sources is another hurdle in the development of wheat cultivars resistant to FHB. Therefore, there is an urgent need to discover novel sources of FHB resistance and introduce them into wheat. This paper reviews the utilization of alien genes to enhance FHB resistance in wheat.

Fusarium head blight resistance in relatives of wheat

Common wheat and durum wheat are two major cultivated species in the genus *Triticum* under the tribe *Triticeae* L. There are over 300 species classified under more than 20 genera in the *Triticeae* (Dewey, 1984). These species carry the genomes homoeologous with the wheat genomes A, B, and D and have variable cross-compatibility with wheat. They represent an invaluable gene pool for wheat improvement. A large number of accessions of wild species related to wheat have been evaluated for FHB resistance since the 1980s. An accession of *Elymus giganteus* L. (syn. *Leymus racemosus* Lam., $2n = 4x = 28$, JJNN) was identified as highly resistant to FHB (Mujeeb-Kazi et al., 1983). Resistance of *E. giganteus* was confirmed by Wang et al. (1986, 1991). High levels of FHB resistance were reported in two *Roegneria* species, *R. kamoji* C. Köch (syn. *Agropyron tsukushiense* Honda, $2n = 6x = 42$, $S^{ts}S^{ts}H^{ts}H^{ts}Y^{ts}Y^{ts}$) and *R. ciliaris* (Trin) Nevski (syn. *A. ciliare* (Trin) Franchet, $2n = 4x = 28$, $S^{c}S^{c}Y^{c}Y^{c}$) (Weng & Liu, 1989, 1991). Both accessions of these two species are native to southern China, which has a warm and humid climate.

A large-scale screening was carried out in *Triticeae* to search for more sources of FHB resistance by Wan et al. (1997a). They evaluated a total of 1507 accessions of 93 species from 18 genera under *Triticeae* and identified 31 accessions with high levels of Type I resistance and 151 accessions with high levels of Type II resistance. These resistant accessions were mainly from the genera *Roegneria, Hystrix, Elymus, Kengyilia*, and *Agropyron* and were collected from different geographical areas of the world (Wan et al., 1997a). In a separate experiment, Wan et al. (1997b) screened 71 accessions of 13 *Roegneria* species for FHB resistance and identified 31 accessions with high levels of Type I and II resistance. These *Roegneria* accessions were mainly collected from Asian warm and subtropical zones with humid climates that favour growth and development of Fusarium pathogens.

Ban (1997) evaluated four indigenous Japanese species in the genus *Elymus* and found that *E. humidus* (Ohwi et Sakamoto) Osada comb. nov. ($2n = 6x = 42$, SSHHYY) and *E. racemifer* (Steud.) Tsvel. ($2n = 4x = 28$, SSYY) were highly resistant to FHB. Fedak (2000) reported that the native Japanese species *E. humidus* was immune to FHB. In our FHB screening experiments, this species exhibited FHB resistance at a level higher than the common wheat cultivar 'Sumai 3', a widely used source of resistance to FHB (Cai & Oliver, unpublished). This is consistent with the results of Ban (1997). Jauhar & Peterson (2001) identified FHB resistance in an accession of *Thinopyrum junceiforme* (Löve & Löve) Löve ($2n = 4x = 28$, $J_1 J_1 J_2 J_2$). Fedak (2000) detected FHB resistance in rye (*Secale cereale* L., $2n = 2x = 14$, RR). We identified three accessions of *Th. intermedium* (Host) Barkworth & D. R. Dewey ($2n = 6x = 42$), two accessions of *Th. ponticum* (Podp.) Barkworth & D. R. Dewey ($2n = 10x = 70$), and one accession of *Th. junceum* (L.) Löve ($2n = 6x = 42$) with Type II FHB resistance equal to that of Sumai 3 in the greenhouse (Figures 1a and 1g) (X. Cai and R. Oliver, unpublished). One accession of *Psatyrostachys huashanica* Keng ($2n = 2x = 14$, *JJ*) native to China, was found to be resistant to FHB (P.D. Chen, unpublished). Most of the wild species accessions evaluated in previous studies have a perennial growth habit and were collected from geographical areas with a climate favorable for epidemics of FHB. It has been suggested that FHB resistance was accumulated in these accessions by gene mutations and natural selection under high disease pressure (Wan et al., 1997a).

Relatives of common and durum wheat in the genus *Triticum* are genetically more closely related to common and durum wheat than the species in other genera under *Triticeae.* Some of the species in *Triticum* share genomes with common and durum wheat and have high crossability with them. These species have been widely exploited for wheat improvement. Resistance to FHB has been found in some of the *Triticum* species. Gagkaeva (2003) identified FHB resistance in 252 accessions of 26 species with various ploidy levels in *Triticum*, including *T. aethiopicum* Jakubz. ($2n = 4x = 28$, AABB), *T. turanicum* Jakubz. ($2n = 4x = 28$, AABB), *T. urartu* Thum. ex Gandil. ($2n = 2x = 14$, AA), *T. timopheevii* (Zhuk.) Zhuk. ($2n = 4x = 28$, AAGG), *T. persicum* Vav. ($2n = 4x = 28$, AABB), *T. ispahanicum* Heslot ($2n = 4x = 28$, AABB), *T. karamyschevii* Nevski ($2n = 4x = 28$, AABB), *T. vavilovii* Jakubz. ($2n = 6x = 42$, AABBDD), *T. dicoccoides* ($2n = 4x = 28$, AABB), *T. sphaerococcum* Perc. ($2n = 6x = 42$, AABBDD), *T. militinae* Zhuk. Et ($2n = 4x = 28$, AAGG), *T. dicoccum* Schrank ($2n = 4x = 28$, AABB), and *T. spelta* L. ($2n = 6x = 42$, AABBDD). It was found that the most resistant accessions were from the species *T. timopheevii*, *T. karamyschevii*, *T. militinae*, *T. persicum, T. dicoccum*, and *T. spelta*. Fedak et al. (2004) also found FHB resistance in *T. monococcum* and *T. timopheevii*.

Figure 1. Reaction to Fusarium head blight of (a) *Triticum aestivum* cv. Sumai 3, (b) *T. aestivum* cv. Chinese Spring (CS), (c) a hexaploid synthetic wheat line (*T. turgidum* cv. Langdon/*T. tauschii*), (d) a CS-*Thinopyrum junceum* disomic addition line, (e) *T. dicoccum*, (f) a partial wheat-*Th. ponticum* amphiploid ($2n = 56$), and (g) *Th. ponticum* (X. Cai, unpublished).

Figure 2. Reaction to Fusarium head blight of *Triticum aestivum* cv. Chinese Spring (CS)-*Leymus racemosus* chromosome translocation lines and their translocated chromosomes. (a) CS, (b) NAU601, a T4BS·4BL-Lr2S translocation line derived from a cross of the ^{60}Co-γ ray irradiated monosomic CS- *L. racemosus* addition line Lr2 with *T. aestivum* cv. Yangmai 5 susceptible to FHB, (c) NAU611, a T4AL·Lr7S(L) translocation line identified from the progeny of the ^{60}Co-γ ray irradiated disomic CS- *L. racemosus* addition line Lr7, (d) *T. aestivum* cv. Sumai 3, (e) C-banded wheat chromosome 4A, C-banded translocated chromosome T4AL·Lr7S(L), translocated chromosome T4AL·Lr7S(L) after FISH, C-banded *L. racemosus* chromosome Lr7 (from left to right), (f) C-banded wheat chromosome 4B, C-banded translocated chromosome T4BS·4BL-Lr2S, translocated chromosome T4BS·4BL-Lr2S after FISH, and C-banded *L. racemosus* chromosome Lr2 (from left to right). Arrowheads indicate translocation points (The chromosome pictures were modified after Chen et al., 1998; the spike pictures are unpublished (P.D. Chen)).

Miller et al. (1998) screened 290 accessions of *T. dicoccoides* for reaction to FHB and identified several accessions with Type II resistance. Screening of 151 *T. dicoccoides* accessions originating from different geographical areas in Israel and Turkey identified eight accessions resistant to FHB although their resistance levels were not as high as Sumai 3 (Buerstmayr et al., 2003). Cai & Xu (unpublished) evaluated 255 accessions of six tetraploid wheat species for Type II FHB resistance, including Persian wheat (*T. carthlicum* (Nevski in Kom.) Á.Löve & D.Löve), wild emmer wheat (*T. dicoccoides*), cultivated emmer wheat (*T. dicoccum*), Polish wheat (*T. polonicum* L.), oriental wheat (*T. turanicum*), and poulard wheat (*T. turgidium*). One Persian wheat and four cultivated emmer accessions exhibited resistance to FHB in that screening experiment (Figures 1a, 1b and 1e). Another evaluation is being carried out to verify the resistance of those tetraploid wheat accessions.

Species in the genus *Aegilops* L. are also closely related to wheat. *Ae. squarrosa* L. ($2n = 2x = 14$, DD) was identified as the most resistant to FHB among the 9 *Aegilops* species, including *Ae. squarrosa* L., *Ae. triuncialis* L. ($2n = 4x = 28$, UUCC), *Ae. cylindrica* Host ($2n = 4x = 28$, CCDD), *Ae. vavilovii* (Zhuk.) Chennav. ($2n = 6x = 42$, DDMMSS), *Ae. juvenalis* (Thell.) Eig ($2n = 6x = 42$, DDMMUU), *Ae. ovata* L. ($2n = 4x = 28$, UUMM), *Ae. crassa* Boiss. ($2n = 4x = 28$, DDMM), *Ae. kotchui* Boiss. ($2n = 4x = 28$, UUSS), and *Ae. bicornis* (Forsk.) Jaub & Spach ($2n = 2x = 14$, SS) evaluated by Gagkaeva (2003). Olivera et al. (2003) evaluated the reaction of 82 *Ae. sharonesis* Eig ($2n = 2x = 14$, S^lS^l) accessions originating from the coastal plain of Israel to FHB and found that 11 of them exhibited high levels of resistance. Fedak et al. (2004) identified 7 *Ae. speltoides* accessions resistant to FHB.

The relatives of wheat identified as resistant to FHB have various ploidy levels, ranging from $2x$ to $10x$, and exhibit different cross-compatibilities with wheat. Some of them contain genomes homologous or closely related to the wheat genomes, such as species in the genera *Triticum* and *Aegilops*, while others do not, such as the species in the genera *Leymus, Thinopyrum, Roegneria, Hystrix, Elymus, Kengyilia,* and *Agropyron*. These species are representatives of the secondary and tertiary gene pools of wheat as classified by Harlan et al. (1973).

Non-homologous chromosomes rarely pair and recombine with each other in the presence of *Ph* genes that inhibit homoeologous pairing in wheat (Sears, 1976, 1984). Thus, transfer of FHB resistance genes to wheat from alien genomes without homology to wheat genomes is more difficult than from alien genomes that are homologous or closely related to the wheat genomes. Special chromosome manipulation is needed to integrate FHB resistance genes into wheat genomes from the non-homologous genomes of alien species.

Transfer of FHB resistance from wild species to wheat

The cultivated wheats, including common wheat and durum wheat, are characterized by allopolyploidy. They are tolerant to aneuploidy and have a large number of wild relatives (Morris & Sears, 1967). These characteristics make it possible to incorporate alien chromatin carrying genes of interest into wheat genomes through chromosome manipulation. A number of genes conferring desirable traits, such as resistance to diseases and insects and tolerance to adverse conditions, have been successfully transferred to wheat from its relatives (Riley et al., 1968; Zeller, 1973; Zeller & Hsam, 1983; Shepherd & Islam, 1988; Jiang et al., 1994b; Jones et al., 1995; Friebe et al., 1996; Cox, 1998; Wang et al., 2003).

Alien chromatin can be introduced into wheat by producing wheat-alien species amphiploids and wheat-alien chromosome addition, substitution, and translocation lines (Sears, 1972; 1981; 1983; Gale & Miller, 1987; Knott, 1987; Feldman, 1988; Shepherd & Islam, 1988). A wheat-alien species amphiploid, combining the genomes of wheat and an alien species, carries a large amount of alien chromatin that usually contains unwanted genes in addition to the gene of interest. Wheat-alien chromosome addition and substitution lines carry an alien chromosome in a wheat genetic background through chromosome addition and substitution, respectively. Chromosome instability and linkage drag on the individual alien chromosomes and meiotic instability limit the utilization of addition and substitution lines in breeding. In addition, alien chromosomes rarely pair and recombine with wheat chromosomes in the presence of the *Ph* genes (Sears, 1976; Feldman, 1988). Therefore, it is difficult for breeders to directly use amphiploids and addition and substitution lines in their breeding programs if a linkage drag exists on the alien chromosome of interest. Inducing translocations between homoeologous wheat and alien chromosomes can minimize linkage drag and has been considered the most effective approach of transferring alien genes to wheat (Jiang et al., 1994b; Friebe et al., 1996).

The species resistant to FHB, *E. giganteus*, *R. ciliaris*, *R. kamoji*, *E. humidus*, *Th. junceiforme*, *Th. ponticum, Th. intermedium*, *Th. junceum*, *P. huashanica*, and *S. cereale* have been successfully hybridized to wheat using immature embryo culture techniques (Wang et al., 1986; Weng & Liu, 1991; Liu et al., 2000c; Jauhar & Peterson, 2001; T. Ban, personal communication; X. Cai, unpublished; P.D. Chen, unpublished). Fusarium head blight resistance in some of these wild species has been transferred to wheat by producing alien chromosome addition, substitution, and translocation lines. From the crosses of wheat with *E. giganteus*, *R. ciliaris,* and *R. kamoji*, a group of scientists at the Institute of Cytogenetics, Nanjing Agricultural University, developed a number of addition and substitution lines of *T. aestivum-L. racemosus, T. aestivum-R. ciliaris,* and *T. aestivum-R. kamoji* (Weng et al., 1995; Qi et al., 1997; Wang et al., 1999; Wang et al., 2001a; Liu, 2002; Chen et al., 2004). Evaluation of these addition and substitution lines for FHB resistance led to identification of three *L. racemosus* chromosomes, one *R. ciliaris* chromosome, and one *R. kamoji* chromosome carrying FHB resistance genes (Chen et al., 1993, 1995; Chen & Liu, 2000; Wang et al., 2001a; Wang et al., 1999). Restriction fragment length polymorphism (RFLP) analysis indicated that two of the three *L. racemosus* chromosomes conferring resistance to FHB belonged to homoeologous groups 5 and 7 (Qi et al., 1997). The *R. ciliaris* and *R. kamoji* chromosomes conferring FHB resistance belonged to the homoeologous groups 1 and 2, respectively (Wang et al., 1999, 2001a).

Jauhar & Peterson (2001) identified derivatives resistant to FHB from a cross between a durum wheat cultivar and a *Th. junceiforme* accession resistant to FHB. The chromosome(s) conferring resistance in the *Th. junceiforme* accession has not been identified. We have developed a number of lines from crosses of the *Th. ponticum* and *Th. intermedium* accessions resistant to FHB with common wheat and durum wheat cultivars. These lines are being evaluated for FHB resistance and characterized using fluorescent *in situ* hybridization (FISH) (X. Cai & S. Xu, unpublished). This will allow identification of the chromosomes conferring FHB resistance in these two *Thinopyrum* species.

Wheat-alien chromosome addition and substitution lines carry an entire alien chromosome and generally cannot be utilized directly in breeding because of linkage drag associated with alien chromosomes and extremely low levels of recombination between wheat and alien chromosomes. Wheat-alien chromosome translocation lines only carry an alien chromosome segment connected with a wheat chromosome and generally have less linkage drag than wheat-alien chromosome addition and substitution lines. In addition, the wheat portion of translocated chromosomes in the translocation lines can recombine with corresponding wheat chromosomes. Therefore, production of wheat-alien chromosome translocation lines is the best approach to utilize alien genes for wheat improvement.

Wheat-alien chromosome translocations can be produced by promoting homoeologous pairing, irradiation, and tissue culture (Morris & Sears, 1967, Sears, 1972; Feldman, 1988). Homoeologous pairing is inhibited by the *Ph* genes in wheat. The *Ph1* gene located on the long arm of chromosome 5B has the most significant effect. Homoeologous pairing can be promoted using the *ph1* mutant (Sears, 1977, 1984), a nullisomic 5B-tetrasomic 5D line in which chromosome 5B is missing (Feldman, 1988), and the *Ph* inhibitor gene (*Ph*^{I}) that suppresses activity of the *Ph* genes (Chen et al., 1994). Gametocidal chromosomes that induce structural variations in chromosomes can also be used to generate wheat-alien chromosome translocations (Endo, 1988). Tissue culture is another approach to induce chromosome translocations for gene transfer (Larkin & Scowcroft, 1981; Lapitan et al., 1984; Larkin et al., 1990). Application of these approaches in inducing translocations between wheat and alien chromosomes could play an important role in the transfer of FHB resistance genes from alien species to wheat.

Chen & Liu (2000) produced 21 *T. aestivum* cv. Chinese Spring (CS)-*L. racemosus* translocation lines from three CS-*L. racemosus* addition lines resistant to FHB using irradiation treatment, the gametocidal chromosome of *Ae. cylindrica*, the *Ph*^{I} gene, and tissue culture. Varied amounts of chromatin from the three *L. racemosus* chromosomes were identified in these translocations using C-banding, FISH, and molecular markers (Chen et al., 1998; Liu et al., 1999; Liu et al., 2000a, b; Zhou et al., 2000; Wang et al., 2001a, b; Yuan et al., 2003). Many of these translocation lines exhibited higher levels of FHB resistance than their wheat parents 'CS' and 'Yangmai 3' (Figures 2a–2c). *L. racemosus* chromatin conferring FHB resistance was detected in the translocation lines (Figures 2b, 2c, 2e and 2f). Some of these translocation lines showed resistance levels as high as Sumai 3. However, resistance levels of the translocation lines carrying a single *L. racemosus* chromosome fragment were lower than those of the original source, *L. racemosus* (Chen & Liu, 2000). Based on these results, it was concluded that resistance in *L. racemosus* was controlled by multiple genes located on at least three *L. racemosus* chromosomes (Chen et al., 1993; Chen & Liu, 2000). Pyramiding of the *L. racemosus* chromosome fragments carrying different resistance genes may lead to the development of wheat lines with better and more durable resistance to FHB.

The CS- *L. racemosus* translocated chromosomes conferring resistance to FHB have been transferred to different common wheat backgrounds. The resultant lines carrying the same translocation in different backgrounds exhibited variable levels of resistance (P. Chen & D. Liu, unpublished). These results demonstrated the variable effect of genetic background on the expression of alien resistance genes in wheat.

Common wheat cultivars and breeding lines resistant to FHB have been developed from the crosses of wheat with rye. They include the Chinese cultivars 'Jinzhou 1', 'Jinzhou 47', and 'Jinzhou 66' (Lu et al., 2000), a US cultivar 'Amigo' (Oliver et al., 2004), and a French line 'Bizel' (Bourdoncle & Ohm, 2003). It is unknown whether these Chinese cultivars carry rye chromatin in their genomes (Lu et al., 2000). Wheat-rye and wheat-*Agropyron elongatum* (Host). Beauv. chromosome translocations were identified in Amigo (Cai, 1994; Jiang et al., 1994a). Detectable rye chromatin was not found in the French line 'Bizel' using rye genome-specific repetitive sequence (Bourdoncle & Ohm, 2003). In addition, resistance to FHB was identified in wheat-rye chromosome addition lines (Fedak, 2000). These results suggested that rye might be a potential source of resistance to FHB for wheat.

Fusarium head blight resistance has been transferred to common wheat from *T. dicoccoides*, *T. timopheevi, T. monococcum, Ae. speltoides,* and synthetic hexaploid wheat lines. A number of common wheat breeding lines resistant to FHB have been developed from the crosses of resistant *T. dicoccoides*, *T. timopheevi, T. monococcum, Ae. speltoides* accessions, and resistant synthetic hexaploid wheat lines with common wheat, respectively (M. Mergoum, personal communication; Fedak et al., 2004). A hard red spring wheat cultivar resistant to FHB, Steele, was developed from the crosses in which a *T. dicoccoides* accession resistant to FHB was involved (Mergoum et al., 2004). In the 1980s, wheat geneticists in the USDA-ARS developed a set of *T. turgidum var. durum* cv. Langdon (LDN)- *T. dicoccoides* accession 'Israel A' (DIC) disomic substitution lines (LDN(DIC)) (Joppa & Cantrell, 1990). Stack et al. (2002) evaluated FHB resistance of these substitution lines in greenhouse and field trials and found the substitution line LDN (DIC-3A) resistant to FHB even though Langdon and Israel A were moderately and highly susceptible to the disease, respectively. Fusarium head blight resistance of LDN (DIC-3A) has been used in breeding for FHB resistance in durum wheat (E. Elias, personal communication). Berzonsky et al. (2004) developed four synthetic hexaploid wheat germplasm lines resistant to FHB by crossing the substitution line LDN (DIC-3A) to four *T. tauschii* accessions. Additional efforts are being made in North Dakota to transfer Fusarium head blight resistance from another *T. dicoccoides* accession to the hard red spring wheat cultivar 'Reeder' (Stack et al., 2003a). *T. dicoccoides* shares A and B genomes with common wheat and synthetic hexaploid wheat lines contain the same genomes as common wheat. Thus, FHB resistance in *T. dicoccoides* and synthetic hexaploid wheat lines can be transferred to wheat via homologous recombination.

Wheat-alien species derivatives resistant to FHB

Numerous crosses have been made between wheat and its relatives to transfer desirable genes to wheat (Sharma & Gill, 1983; Jiang et al., 1994b; Sharma, 1995). A large number of wheat-alien species derivatives have been produced from these crosses, including wheat-alien species amphiploids and wheat-alien chromosome addition, substitution, and translocation lines (Shepherd & Islam, 1988). Genes conditioning desirable agronomic traits have been identified in these derivatives (Wong et al., 1974; Thomas & Conner, 1986; Shepherd & Islam, 1988; Mukai et al., 1993; Raupp et al., 1993; Jones et al., 1995; Friebe et al., 1996; Cai et al., 1996; 1998). Wheat-alien species derivatives produced in previous studies could serve as a novel source of resistance to FHB for wheat.

We screened over 300 wheat-alien species derivatives for Type II FHB resistance in the greenhouse. Seventy-four of them were identified as resistant to FHB. Some of the 74 resistant derivatives exhibited resistance comparable to Sumai 3 (Oliver et al., 2004). There were wheat-alien species amphiploids, wheat-alien chromosome substitution and translocation lines, synthetic hexaploid wheat lines (durum wheat-*Ae. squarrosa* amphiploids), and the lines with unknown chromosome constitutions among the resistant derivatives (Figures 1c, d and 1f). The alien species involved in these derivatives included *Ae. squarrosa*, *R. kamoji*, *R. ciliaris*, *L. racemosus, Th. ponticum*, *Th. elongatum* (Host) D.R. Dewey ($2n = 2x = 14$, EE), *Th. junceum, Th. intermedium*, *Dasypyrum villosa* L., and *S. cereale* (Oliver et al., 2004). A number of synthetic hexaploid wheat lines were reported as resistant to FHB and were released by the International Maize and Wheat Improvement Centre (CIMMYT). We found that some of them did not exhibit resistance in our FHB screening experiments (X. Cai & S. Xu, unpublished). Su et al. (2000) also reported FHB resistance in synthetic hexaploid wheat lines. Some resistant wheat-alien chromosome translocation lines and synthetic hexaploid wheat lines have a great potential to be utilized directly in developing wheat cultivars resistant to FHB. We have been manipulating chromosomes in the resistant wheat-alien species amphiploids and substitution lines to eliminate unwanted alien chromatin from these lines. This allows for reducing linkage drag on the alien chromosomes of interest and developing elite breeding lines resistant to FHB.

Evaluation of durum wheat-*Th. distichum* (Thunb.) Löve ($2n = 4x = 28$) derivatives for FHB resistance identified two lines resistant to FHB, which carried 13 and 22 *Th. distichum* chromosomes, respectively (Chen et al., 2001). Fedak et al. (2003) found that chromosome $1H^{ch}$ of *Hordeum chilense* Roem. et Schult. ($2n = 2x = 14$, $H^{ch}H^{ch}$) and chromosome 7E of *Th. elongatum* conferred resistance to FHB in the genetic background of common wheat cultivar Chinese Spring (CS). Resistance conferred by *Th. elongatum* chromosome 7E was confirmed by Shen et al. (2004). Three partial *T. turgidum* var. *durum*-tetraploid *Th. elongatum* amphiploids were identified to have 14 *Th. elongatum* chromosomes and exhibited resistance to FHB (Han & Fedak, 2003). A number of wheat- *Th. bessarabicum* Löve derivatives were developed and FHB resistance was detected from these derivatives (Chen & Liu, unpublished). All these wheat-alien species derivatives are desirable 'bridge' materials for transferring FHB resistance to wheat from the alien species through chromosome manipulation.

Two sets of LDN-*T. dicoccoides* disomic substitution lines were recently developed using two resistant *T. dicoccoides* accessions as chromosome donors (Joppa, unpublished; Xu et al., 2004). Evaluation of these substitution lines for reaction to FHB in the greenhouse indicated that chromosomes 5B and 7A in the *T. dicoccoides* accessions conferred resistance to FHB (Stack et al., 2003b). Effective resistance to FHB has not been found in durum wheat. These resistant substitution lines carrying only one *T. dicoccoides* chromosome in a durum background could be utilized to enhance resistance of durum wheat to FHB.

Conclusions

Relatives of wheat represent potential sources of novel resistance to FHB for wheat. Fusarium head blight resistance can be transferred to wheat from alien species via homologous chromosome pairing, induced chromosome pairing or by chromosome manipulations that lead to translocations. The most effective approach to introduce FHB resistance into wheat from alien species is to integrate alien chromosomal fragments that carry the resistance genes and do not confer significant linkage drag on wheat genomes through translocations. Since none of the derived lines are highly resistant to FHB, pyramiding of the alien resistance genes in wheat may be necessary to develop wheat cultivars with high levels of durable resistance to FHB.

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References

Bai, G.H., R. Plattner, A. Desjardins & F. Kolb, 2001. Resistance to Fusarium head blight and deoxynivalenol accumulation in wheat. Plant Breed 120: 1–6.

Ban, T., 1997. Evaluation of resistance to *Fusarium* head blight in indigenous Japanese species of *Agropyron (Elymus)*. Euphytica 97: 39–44.

Berzonsky, W.A., K.D. Hartel, S.F. Kianian & G.D. Leach, 2004. Registration of four synthetic hexaploid wheat germplasm lines with resistance to Fusarium head blight. Crop Sci 44: 1500–1501.

Bourdoncle, W. & H.W. Ohm, 2003. Fusarium head blight-resistant wheat line 'Bizel' does not contain rye chromatin. Plant Breed 122: 281–282.

Buerstmayr, H., M. Stierschneider, B. Steiner, M. Lemmens, M. Griesser, E. Nevo & T. Fahima, 2003. Variation for resistance to head blight caused by *Fusarium graminearum* in wild emmer (*Triticum dicoccoides*) originating from Israel. Euphytica 130: 17–23.

Cai, X., 1994. Chromosome translocations in the common wheat variety 'Amigo'. Hereditas 121: 199–202.

Cai, X., S.S. Jones & T.D. Murray, 1996. Characterization of an *Agropyron elongatum* chromosome conferring resistance to Cephalosporium stripe in common wheat. Genome 39: 56–62.

Cai, X., S.S. Jones & T.D. Murray, 1998. Molecular cytogenetic characterization of *Thinopyrum* and wheat-*Thinopyrum* translocated chromosomes in a wheat-*Thinopyrum* amphiploid. Chromosome Research 6: 183–189.

Chen, P.D. & D.J. Liu, 2000. Transfer scab resistance from *Lemus racemosus, Roegneria ciliaris,* and *Roegneria kamoji* into common wheat. In: W.J. Raupp, Z. Ma, P.D. Chen & D.J. Liu (Eds.), Proc Int Symp Wheat Improv Scab Resist, Suzhou and Nanjing, China, pp. 62–67.

Chen, P.D., W.X. Liu, J.H. Yuan, Y.G. Feng, S.L. Wang, X. Wang, B. Zhou, S.Z. Zhang, G.X. Liu & D.J. Liu, 2004. Development and utilization of alien translocation lines for wheat scab resistance improvement. In: S.M. Canty, T. Boring, K. Versdahl, J. Wardwell, & R.W. Ward (Eds.), Proc. 2nd Intern Symp on Fusarium Head Blight, Orlando, pp. 33–36.

Chen, P.D., Z.T. Wang, S.L. Wang, L. Huang, Y.Z. Wang & D.J. Liu, 1993. Transfer of wheat scab resistance from *Elymus giganteus* into common wheat In: Z.S. Li & Z.Y. Xin (Eds.), Proc 8th Int Wheat Genet Symp, China Agri Sci Press, Beijing, pp. 153–157.

Chen, P.D., Z.T. Wang, S.L. Wang, L. Huang, Y.Z. Wang & D.J. Liu, 1995. Transfer of useful germplasm for *Leymus racemosus* Lam. to common wheat. Development of addition lines with wheat scab resistance. Acta Genetica Sinica 22: 380–386 (in Chinese with English abstract).

Chen, P.D., W. Sun, W. Liu, Z. Liu, S. Wang & D.J. Liu, 1998. Development of wheat-*Leymus racemosus* translocation lines with scab resistance. In: A.E. Slinkard (Ed.), Proc 9th Int Wheat Genet Symp, University of Saskatchewan, University Extension Press, Saskatoon, Saskatchewan, Canada, pp. 32–34.

Chen, P.D., H. Tsujimoto & B.S. Gill, 1994. Transfer of Ph^1 genes promoting homoeologous pairing from *Triticum speltoides* to common wheat. Theor Appl Genet 88: 97–101.

Chen, Q., F. Eudes, R.L. Conner, R. Graf, A. Comeau, J. Collin, F. Ahmad, R. Zhou, H. Li, Y. Zhao & A. Laroche, 2001. Molecular cytogenetic analysis of a durum wheat X *Thinopyrum distichum* hybrid used as a new source of resistance to Fusarium head blight in the greenhouse. Plant Breed 120: 375–380.

Cox, T.S., 1998. Deepening the wheat gene pool. J Crop Prod 1: 1–25.

Dewey, D.R., 1984. The genomic system of classification as a guide to intergeneric hybridization with the perennial *Triticeae*. In: J.P. Guastafson (Ed.), Gene Manipulation in Plant Improvement, 16th Stadler Genet Symp, Lenum Press, New York, pp. 209–279.

Endo, T.R., 1988. Induction of chromosomal structural changes by a chromosome of *Aegilops cylindrica* L. in common wheat. J Hered 79: 366–370.

Fedak, G., 2000. Sources of resistance to Fusarium head blight. In: W.J. Raupp, Z. Ma, P.D. Chen & D.J. Liu (Eds.), Proc Int Symp Wheat Improv Scab Resist, Suzhou and Nanjing, China, pp. 4.

Fedak, G., W. Cao, F. Han, M. Savard, J. Gilbert & A. Xue, 2004. Germplasm enhancement for FHB resistance in spring wheat through alien introgression. In: S.M. Canty, T. Boring, K. Versdahl, J. Wardwell & R.W. Ward (Eds.), Proc. 2nd Int Symp on Fusarium Head Blight, Orlando, Michigan State University, East Lansing, MI, pp. 56–57.

Fedak, G., F. Han, W. Cao, M. Burvill, S. Kriteno & L. Wang, 2003. Identification and characterization of novel sources of resistance to *Fusarium* head blight. In: N.E. Pogna, M. Romano, E.A. Pogna & G. Galterio (Eds.), Proc. 10th Int Wheat Genet Symp I. Istituto Sperimentale per la Cerealicoltura, Rome, Italy, pp. 354–356.

Feldman, M., 1988. Cytogenetic and molecular approaches to alien gene transfer in wheat. In: T.E. Miller & R.M.D. Koebner (Eds.), Proc 7th Int Wheat Genet Symp, Cambridge, England, pp. 23–32.

Friebe, B., J. Jiang, W.J. Raupp, R.A. McIntosh & B.S. Gill, 1996. Characterization of wheat-alien translocations conferring resistance to diseases and pests: Current status. Euphytica 91: 59–87.

Gagkaeva, T.Y., 2003. Importance of Fusarium head blight in Russia and the search for new sources of genetic resistance in wheat and barley. In: S.M. Canty, J. Lewis & R.W. Ward (Eds.), 2003 National Fusarium Head Blight Forum Proc, U.S. Wheat & Barley Scab Initiative, pp. 219–222.

Gale, M.D. & T.E. Miller, 1987. The introduction of alien genetic variation into wheat. In: F.G.H. Lupton (Ed.), Wheat Breeding: Its Scientific Basis. Chapman and Hall, UK, pp. 173–210.

Han, F. & G. Fedak, 2003. Molecular characterization of partial amphiploids from *Triticum durum* x tetraploid *Thinopyrum elongatum* as novel sources of resistance to wheat Fusarium head blight. In: N.E. Pogna, M. Romano, E.A. Pogna, & G. Galterio (Eds.), Proc 10th Int Wheat Genet Symp III. Istituto Sperimentale per la Cerealicoltura, Rome, Italy, pp. 1148–1150.

Harlan, J.R., M.J. de Wet & E.G. Price, 1973. Comparative evolution of cereals. Evolution 27: 311–325.

Jauhar, P.P. & T.S. Peterson, 2001. Hybrids between durum wheat and *Thinopyrum junceiforme*: Prospects for breeding for scab resistance. Euphytica 118: 127–136.

Jiang, J., B. Friebe & B.S. Gill, 1994a. Chromosome painting of Amigo wheat. Theor Appl Genet 89: 811–813.

Jiang, J., B. Friebe & B.S. Gill, 1994b. Recent advances in alien gene transfer in wheat. Euphytica 73: 199–212.

Jones, S.S., T.D. Murray & R.E. Allan, 1995. Use of alien genes for the development of disease resistance in wheat. Annu Rev Phytopathol 33: 429–443.

Joppa, L.R. & R.G. Cantrell, 1990. Chromosomal location of genes for grain protein content of wild tetraploid wheat. Crop Sci 30: 1059–1064.

Knott, D.R., 1987. Transferring alien genes to wheat. In: E.G. Heyne (Ed.), Wheat and Wheat Improvement (2nd edn.), ASA-CSSA-SSSA, Madison, WI, pp. 462–471.

Lapitan, N.L.V., R.G. Sears & B.S. Gill, 1984. Translocations and other karyotypic structural changes in wheat x rye hybrids regenerated from tissue culture. Theor Appl Genet 68: 547–554.

Larkin, P.J. & W.R. Scowcroft, 1981. Somaclonal variation - a novel source of variability from cell cultures for plant improvement. Theor Appl Genet 60: 197–214.

Larkin, P.J., L.H. Spindler & P.M. Banks, 1990. The use of cell culture to restructure plant genomes for introgressive breeding. In: G. Kimber (Ed.) Proc 2nd Int Symp Chromo Engi in Plants, University of Missouri, Columbia, Missouri, pp. 80–89.

Liu, D.J., 2002. Genome analysis in wheat breeding for disease resistance. Acta Botanica Sinica 44: 1096–1104.

Liu, W.X., P.D. Chen & D.J. Liu, 1999. Studies of the development of *Triticum aestivum-Leymus racemosus* translocation lines by pollen irradiation. Acta Genetica Sinica 27: 44–49 (in Chinese with English abstract).

Liu, W.X., P.D. Chen & D.J. Liu, 2000a. Development of *Triticum aestivum-Leymus racemosus* translocation lines by irradiating adult plants at meiosis. Acta Botanica Sinica 41: 463–467 (in Chinese with English abstract).

Liu, W.X., P.D. Chen & D.J. Liu, 2000b. Selection, breeding and identification of *Triticum aestivum-Leymus racemosus* translocation line. Acta Agronomica Sinica 26: 305–309 (in Chinese with English abstract).

Liu, Z.H., X. Zhang, J.X. Yao & W.Z. Lu, 2000c. A new scab-resistant line and its cytogenetic study. In: W.J. Raupp, Z. Ma, P.D. Chen & D.J. Liu (Eds.), Proc Int Symp Wheat Improv Scab Resist, Suzhou and Nanjing, China, pp. 38–41.

Lu, W.Z., S.H. Cheng & R.Z. Wang, 2000. Evaluation of wheat and its relatives for Fusarium head blight resistance. In: Lu, W.Z., S.H. Cheng & R.Z. Wang (Eds.), Studies of Fusarium Head Blight Resistance in Wheat (in Chinese with English abstract), China Agri Press, Beijing, pp. 61–67.

McMullen, M., R. Jones & D. Gallenberg, 1997. Scab of wheat and barley: Are-emerging disease of devastating impact. Plant Dis 81: 1340–1348.

Mentewab, A., H.N. Rezanoor, N. Gosman, A.J. Worland & P. Nicholson, 2000. Chromosomoal location of *Fusarium* head blight resistance genes and analysis of the relationship between resistance to head blight and brown foot rot. Plant Breed 119: 15–20.

Mergoum, M., R.C. Frohberg, J.D. Miller & R.W. Stack, 2004. Registration of ‘Steele-ND’ wheat. Crop Sci (submitted).

Mesterhazy, A., 1995. Types and components of resistance to Fusarium head blight of wheat. Plant Breed 114: 377–386.

Miller, J.D., R.W. Stack & L.R. Joppa, 1998. Evaluation of *Triticum turgidum* L. var. *dicoccoides* for resistance to Fusarium head blight and stem rust. In: A.E. Slinkard (Eds.), Proc 9th Int Wheat Genet Symp, University of Saskatchewan, University Extension Press, Saskatoon, Saskatchewan, Canada, pp. 292–293.

Morris, R. & E.R. Sears, 1967. The cytogenetics of wheat and its relatives. In: K.S. Quisenberry & L.P. Reitz (Eds.), Wheat and Wheat Improvement, ASA-CSSA-SSSA, Madison, WI, pp. 19–87.

Mujeeb-Kazi, A., M. Bernard, G.T. Bekele & J.L. Mirand, 1983. Incorporation of alien genetic information from *Elymus giganteus* into *Triticum aestivum*. In: S. Sakamoto (Ed.), Proc 6th Int Wheat Genet Symp Maruzen, Kyoto, Japan, pp. 223–231.

Mukai, Y., B. Friebe, J.H. Hatchett, M. Yamamoto & B.S. Gill, 1993. Molecular cytogenetic analysis of radiation-induced wheat-rye terminal and intercalary chromosomal translocations and the detection of rye chromatin specifying resistance to Hessian fly. Chromosoma 102: 88–95.

Nganje, W.E., D.D. Johnson, W.W. Wilson, F.L. Leistritz, D.A. Bangsund & N.M. Tiapo, 2001. Economic impacts of Fusarium head blight in wheat and barley: 1998–2000. Agribusiness & Applied Economics Report No. 464: 1–41.

Oliver, R.E., X. Cai, S.S. Xu, X. Chen & R.W. Stack, 2004. Wheat-alien species derivatives: a novel source of resistance to Fusarium head blight in wheat. Crop Sci (accepted).

Olivera, P., B. Steffenson & Y. Anikster, 2003. Reaction of *Aegilops sharonesis* to Fusarium head blight. In: S.C. Canty, J. Lewis & R.W. Ward (Eds.), 2003 National Fusarium Head Blight Forum Proc, U.S. Wheat & Barley Scab Initiative, pp. 226 (abstract).

Qi, L.L., S.L. Wang, P.D. Chen, D.J. Liu, B. Friebe & B.S. Gill, 1997. Molecular cytogenetic analysis of *Leymus racemosus* chromosomes added to wheat. Theor Appl Genet 95: 1048–1091.

Riley, R., V. Chapman & R. Johnson, 1968. Introduction of yellow-rust resistance of *Aegilops comosa* into wheat by genetically induced homoeologous recombination. Nature 217: 383–384.

Raupp, W.J., A. Amri, J.H. Hatchett, B.S. Gill, D.L. Wilson & T.S. Cox, 1993. Chromosomal location Hessian fly-resistance genes *H22, H23*, and *H24* derived from *Triticum tauschii* in the D genome of wheat. J Hered 84:142–145.

Rudd, J.C., R.D. Horsley, A.L. McKendry & E.M. Elias, 2001. Host plant resistance genes for Fusarium head blight: Sources, mechanisms, and utility in conventional breeding systems. Crop Sci 41: 620–627.

Schroeder, H.W. & J.J. Christensen, 1963. Factors affecting resistance of wheat to scab caused by *Gibberella zeae*. Phytopathology 53: 831–838.

Sears, E.R., 1972. Chromosome engineering in wheat. In: Stadler Symposia, Vol 4. Univ of Missouri, Columbia, pp. 23–38.

Sears, E.R., 1976. Genetic control of chromosome pairing in wheat. Ann Rev Genet 10: 31–51.

Sears, E.R., 1977. An induced mutant with homoeologous pairing in common wheat. Can J Genet Cytol 19: 585–593.

Sears, E.R., 1981. Transfer of alien genetic material to wheat. In: L.T. Evans & W.J. Peacock (Eds.), Wheat Science-Today and Tomorrow. Cambridge University Press, Cambridge, pp. 75–89.

Sears, E.R., 1983. The transfer to wheat of interstitial segments of alien chromosomes. In: S. Sakamoto (Ed.), Proc 6th Int Wheat Genet Symp, Kyoto, Japan, pp. 5–12.

Sears, E.R., 1984. Mutations in wheat that raise the level of meiotic chromosome pairing. In: J.P. Gustafson (Ed.), Manipulation in Plant Improvement, Plenum Press, New York, pp. 295–300.

Sharma, H.C., 1995. How wide can a wide cross be? Euphytica 82: 43–64.

Sharma, H.C. & B.S. Gill, 1983. New hybrids between *Agropyron* and wheat. 2. Production, morphology and cytogenetic analysis of F_1 hybrids and backcross derivatives. Theor Appl Genet 66: 111–121.

Shen, X., L. Kong & H. Ohm, 2004. Fusarium head blight resistance in hexaploid wheat (*Triticum aestivum*)-*Lophopyrum* genetic lines and tagging of the alien chromatin by PCR markers. Theor Appl Genet 108: 808–813.

Shepherd, K.W. & A.K.M.R. Islam, 1988. Fourth compendium of wheat-alien chromosome lines. In: T.E. Miller & R.M.D. Koebner (Eds.), Proc 7th Int Wheat Genet Symp, Cambridge, England, pp. 1373–1398.

Stack, R.W., E.M. Elias, F.J. Mitchell, J.D. Miller & L.R. Joppa, 2002. Fusarium head blight reaction of Langdon durum-*Triticum dicoccoides* chromosome substitution lines. Crop Sci 42: 637–642.

Stack, R.W., R.C. Frohberg, J.M. Hansen & M. Mergoum, 2003a. Transfer and expression of resistance to Fusarium head blight from wild emmer chromosome 3A to bread wheat. In: S.C. Canty, J. Lewis & R.W. Ward (Eds.), National Fusarium Head Blight Forum Proc, U.S. Wheat & Barley Scab Initiative, pp. 232 (abstract).

Stack, R.W., J.D. Miller & L.R. Joppa, 2003b. A wild emmer having multiple genes for resistance to Fusarium head blight. In: N.E. Pogna, M. Romano, E.A. Pogna & G. Galterio (Eds.), Proc. 10th Int Wheat Genet Symp I. Istituto Sperimentale per la Cerealicoltura, Rome, Italy, pp. 1257–1259.

Su, L., Q. Song & S. Qi, 2000. A preliminary study on the application of synthetic hexaploid wheat derived from ‘*T. durum/Ae. Tauschii*’ crosses in common wheat for Fusarium head blight resistance. In: W.J. Raupp, Z. Ma, P.D. Chen & D.J. Liu (Eds.), Proc Int Symp Wheat Improv Scab Resist, Suzhou and Nanjing, China, pp. 42–46.

Thomas, J.B. & R.L. Conner, 1986. Resistance to colonization by the wheat curl mite in *Aegilops squarrosa* and its inheritance after transfer to common wheat. Crop Sci 26: 527–530.

Wan, Y.F., C. Yen & J.L. Yang, 1997a. The diversity of head-scab resistance in *Triticeae* and their relation to ecological conditions. Euphytica 97: 277–281.

Wan, Y.F., C. Yen, J.L. Yang & L.F. Quan, 1997b. Evaluation of *Roegneria* for resistance to head scab caused by *Fusarium graminearum* Schwabe. Genetic Resources & Crop Evolution 44: 211–215.

Wang, R.R.C., X.M. Li, Z.M. Hu, J.Y. Zhang, S.R. Larson, X.Y. Zhang, C.M. Grieve & M.C. Shannon, 2003. Development of salinity-tolerant wheat recombinant lines from a wheat disomic addition line carrying a *Thinopyrum junceum* chromosome. Int J Plant Sci 164: 25–33.

Wang, Y.N., P.D. Chen & D.J. Liu, 1986. Transfer of useful germplasm from *Elymus giganteus* L. to common wheat. I. Production of (*T. aestivum* L. cv. Chinese Spring x *E. giganteus*)F_1. J Nanjing Agri Univ 9: 10–14 (in Chinese with English abstract).

Wang, X.E., P.D. Chen, D.J. Liu, P. Zhang, B. Zhou, B. Friebe & B.S. Gill, 2001a. Molecular cytogenetic characterization of *Roegneria ciliaris* chromosome additions in common wheat. Theor Appl Genet 102: 651–657.

Wang, X.E., P.D. Chen, B. Zhou, J.H. Yuan, W.X. Liu, B.S. Gill & D.J. Liu, 2001b. RFLP analysis of wheat-*L. racemosus* translocation lines. Acta Genetica Sinica 28: 1142–1150.

Wang, Y.N., P.D. Chen, Z.T. Wang & D.J. Liu, 1991. Transfer of useful germplasm from *Elymus giganteus* L. to common wheat. II. Cytogenetics and scab resistance of backcross derivatives. J Nanjing Agri Univ 14: 1–5 (in Chinese with English abstract).

Wang, Y.Z. & J.D. Miller, 1988. Screening techniques and sources of resistance to Fusarium head blight. In: A.R. Klatt (Ed.), Wheat Production Constraints in Tropical Environments. CIMMYT, Mexico, pp. 239–250.

Wang, S.L., L.L. Qi, P.D. Chen, D.J. Liu, B. Friebe & B.S. Gill, 1999. Molecular cytogenetic identification of wheat-*Elymus tsukushiense* introgression lines. Euphytica 107: 217–224.

Weng, Y.Q. & D.J. Liu, 1989. Morphology, scab resistance and cytogenetics of intergeneric hybrids of *Triticum aestivum* L. with *Roegneria* C.Koch species. Scientia Agricultura Sinica 22: 1–7 (in Chinese with English abstract).

Weng, Y.Q. & D.J. Liu, 1991. Morphological and cytological investigation of interspecific hybrids between *Roegneria ciliaris, R. japonensis*, and *R. kamoji*. J Nanjing Agri Univ 14:1–5 (in Chinese with English abstract).

Weng, Y.Q., L.F. Wu, P.D. Chen & D.J. Liu, 1995. Development of alien addition line of wheat with scab resistance from *Roegneria kamoji* C. Koch. In: Z.S. Li & Z.Y. Xin (Eds.), Proc 8th Int Wheat Genet Symp, Beijing, China, China Agri Press, pp. 365–368.

Windels, C.E., 2000. Economic and social impacts of Fusarium heat blight: Changing farms and rural communities in the northern great plains. Phytopathology 90: 17–21.

Wong, R.S., D.G. Wells & W.S. Gardner, 1974. Cytogenetics and breeding behavior of a hexaploid Agrotricum immune from wheat streak mosaic virus. Crop Sci 14: 406–407.

Xu, S.S., K. Khan, D.L. Klindworth, J.D. Faris & G. Nygard, 2004. Chromosomal locations of genes or novel glutenin subunits and gliadins in wild emmer wheat (*Triticum tugidum* L. *var. dicoccoides*). Theor Appl Genet 108: 1221–1228.

Yuan, J.H., P.D. Chen & D.J. Liu, 2003. Inducing *Triticum aestivum-Leymus racemosus* chromosome translocations using a gametocidal chromosome. Science in China 46: 522–530.

Zeller, F.J., 1973. 1B/1R wheat-rye chromosome substitutions and translocations. In: E.R. Sears & L.M.S. Sears (Eds.), Proc 4th Int Wheat Genet Symp, Univ of Missouri, Columbia, USA, pp. 209–221.

Zeller, F.J. & S.L.K. Hsam, 1983. Broadening the genetic variability of cultivated wheat by utilizing rye chromatin. In: S. Sakamoto (Ed.), Proc 6th Int Wheat Genet Symp, Kyoto, Japan, pp. 161–173.

Zhou, B., X. Wang, P.D. Chen, D.J. Liu, B. Friebe & B.S. Gill, 2000. Molecular cytogenetic characterization of wheat-*Leymus racemosus* translocation lines. In: W.J. Raupp, Z. Ma, P.D. Chen & D.J. Liu (Eds.), Proc Int Symp Wheat Improv Scab Resist, Suzhou and Nanjing, China, pp. 68–72.